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Research Article

Primitive new termites (Blattodea, Termitoidae) in Cretaceous amber from Myanmar

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Abstract

Mastotermitidae, the first-diverging extant family of termites, has only one relic extant species; however, this family had greater richness during the Mesozoic and Cenozoic eras. Fossil termites from the Cretaceous provide information on the early evolution of termites and the transition between extinct families. Herein, two new Mastotermitidae species found in upper Cretaceous (Cenomanian) Kachin amber are reported. One is a female imago described as *Angustitermes reflexus* **gen. et sp. nov.** and assigned to the subfamily Mastotermitinae. The other is *Mastotermes reticulatus* **sp. nov.**, which is described from an isolated forewing. With the comparison especially of the antenna and venation, these new mastotermitids further increase our knowledge of the diversity and morphology of Mastotermitidae during the Mesozoic.

Key words: Fossil termites, Isoptera, Mastotermitidae, social insects, taxonomy

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Introduction

Termites are social insects with the support of mutualistic protists or cellulose-digesting bacteria (Breznak and Brune 1994; Sanderson 1996; Sugimoto et al. 2000; Krishna et al. 2013a; Zhao et al. 2020, 2021). The enormous biomass of termites largely contributes to the global carbon cycle, while occupying an important ecological position in the biosphere (Tuma et al. 2020). The rank of termites has been controversial. Inward et al. (2007) indicated that the rank of termites should be a family, however, some termitologists proposed to continue using "Isoptera" (Lo et al. 2007), and the current compromise is to use "epifamily Termitoidae" (Eggleton et al. 2007; Bignell et al. 2011; Xiao et al. 2012; Beccaloni and Eggleton 2013; Zhao et al. 2019) or "infraorder Isoptera".

As the first-diverging extant family in Termitoidae (Thompson et al. 2000; Legendre et al. 2015; Bucek et al. 2019; Zhao et al. 2019), Mastotermitidae

shares many characters with cockroaches, for example, a large anal lobe in the hind wing and vestigial ootheca or egg pod (Nalepa and Lenz 2000; Krishna et al. 2013a). The most obvious morphological differences from other termite families are that the hind wings have large anal lobes and Sc, R, Rs, and M veins are thick and more sclerotized than CuA. Mastotermitidae was divided into two subfamilies, Mastotermitinae Desneux, 1904 and Idanotermitinae Engel, 2021, based on the presence or absence of ocelli (Jiang et al. 2021).

Besides the sole relic species, *Mastotermes darwiniensis* Froggatt, 1897, living in northern Australia and southern New Guinea (Froggatt 1897; Nalepa and Lenz 2000; Engel et al. 2009), nine genera and 33 extinct species have been documented. Among them, 21 species were documented from compression fossils, one from Cretaceous deposits, and others from Cenozoic deposits (e.g. Wappler and Engel 2006; Krishna et al. 2013b; Vršanský and Aristov 2014; Engel et al. 2015; Bezerra et al. 2020). In addition, 12 species were reported in amber, among which seven species were reported from the Cretaceous, including five species from Kachin amber (Zhao et al. 2019; Jouault et al. 2021, 2022): *Anisotermes bourguignoni* Jouault, Engel, Huang & Nel, 2022, *Anisotermes xiai* Zhao, Eggleton & Ren, 2019, *Magnifitermes krishnai* Jouault, Engel & Nel, 2022, *Mastotermes monostichus* Zhao, Eggleton & Ren, 2019, *Mastotermes myanmarensis* Jouault, 2022, *Milesitermes engeli* Jouault & Nel, 2021, one species from amber of Sagaing Region, Myanmar: *Mastotermes myanmarensis* Jouault, 2022 (Jouault et al. 2022). One species was described from France: *Mastotermes sarthensis* Schlüter, 1989 (Schlüter 1989). The other five species were reported from the Cenozoic (Krishna and Emerson 1983; Krishna and Grimaldi 1991; Nel and Bourguet 2006; Engel et al. 2007; Engel 2008).

Materials and methods

The two specimens studied here were collected from amber mines located in the Hukawng Valley in Kachin State of northern Myanmar. Determined by U-Pb dating of Zircon, the deposit age of the amber mine was 98.79 ± 0.62 Ma which means it comes from early Cenomanian of the upper Cretaceous (Shi et al. 2012). The amber specimens involved in this study were acquired by Mr Fangyuan Xia before 2015 and donated for this study in 2016. Both specimens are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (**CNUB**, curator: Dong Ren).

The amber is cut and polished. The specimens are examined, measured, and photographed with a Nikon SMZ25 microscope system. To help reduce picture distortion caused by refraction and internal cracks, the amber was placed in a properly sized crystallizing dish, with a proper amount of water, and the capture angle and area of interest was adjusted when viewing; the amber was affixed with plasticine when measurements and photographs were taken.

All images are stacked using the software Helicon Focus v. 8 for better depth of field. Simplified drawings were prepared using Adobe Illustrator CC and further modified using Adobe Photoshop CC.

Systematic paleontology

Family Mastotermitidae Desneux, 1904
Subfamily Mastotermitinae Engel, 2021

Genus *Angustitermes* Jiang, Z.Zhao & Ren, gen. nov.
https://zoobank.org/FA73A948-C6EE-43D2-86E9-09485B5F7970

Type species. *Angustitermes reflexus* Jiang, Z. Zhao & Ren, gen. et sp. nov. (Figs 1–3).

Etymology. *Angusti-* is a Latin adjective, reflecting the fact that the medial field of this genus is narrow, and *termes* is the usual noun for the generic name in Termitoidae. The gender is masculine.

Diagnosis. Imago: ocelli oval; fontanelle absent; Y-suture absent; mandibles not exceeding labrum; antenna moniliform with 22 articles; compound eyes lying in middle position on head; pronotum saddle-shaped. Wings heavily reticulated, with "cross-veins" present. **Forewing:** scale large, overlapping hind wing base, humeral suture convex; all major veins origin in scale; veins Sc, R_1, R_2, Rs, and M more pigmented than CuA; Sc simple; Rs with about three main branches, terminating on costal margin anterior to wing apex; radial field narrow, parallel to costal margin; M closer to Rs than CuA, lying more or less parallel to Rs as a simple vein for the greater part of its length, first branching in apical 1/5 of wing length, medial field narrow, encompassing wing apex; CuA branched, lying above the mid-longitudinal line of wing; CuP (claval suture) arched, meeting basal suture before posterior margin. **Hind wing:** basal suture not visible, large anal lobe present. **Legs:** tibial spines of all legs present; tibial spur formula 3–4–4; tarsi pentamerous; arolium present. **Abdomen:** cerci short, trimerous; abdominal styli absent.

Remarks. Based on the sclerotized vein M, presence of the anal lobe, saddle-shaped pronotum, pentamerous tarsi, etc., *Angustitermes* gen. nov. is considered to belong to the Mastotermitidae and is assigned to the subfamily Mastotermitinae because of the ocelli (Fig. 1C). Besides the new genus and *Mastotermes*, there are two other genera in Mastotermitinae: *Garmitermes* Engel, Grimaldi & Krishna, 2007 and *Magnifitermes* Jouault, Engel & Nel, 2022. Termites in both *Angustitermes* gen. nov. and *Garmitermes* have a rounded head, but unlike *Angustitermes* gen. nov., *Garmitermes* has 26 antennal articles, the arolium is greatly vestigial or absent, and the tibial spur formula of *Garmitermes* is 3–5–4 (Engel et al. 2007). Both *Angustitermes* gen. nov. and *Magnifitermes* have arolium, and their tibial spur formula is the same. However, the shape of the head of *Magnifitermes* is relatively long and with about 28 antennal articles (Jouault et al. 2022). Although in different subfamilies, *Angustitermes* gen. nov. and *Anisotermes* share many similarities, such as the rounded head and the tibial spur formula. However, the M vein of *Anisotermes* is located halfway between Rs and CuA, and the first inferior branch of the M vein on the hind wings gradually fades away, ultimately terminating in the center of the hind wings of *Anisotermes* (Zhao et al. 2019; Jouault et al. 2022).

The major feature of *Angustitermes* gen. nov. is that the M vein is a simple vein for the greater part of its length, first branch branching in the apical 1/5 of wing length, and the medial field is narrow (Fig. 2B). The simple M and narrow medial field of *Angustitermes* gen. nov. is similar to *Blattotermes* Riek, 1952. However, *Angustitermes* gen. nov. has sparser veins than *Blattotermes*; the

branches of R and secondary branches of CuA are fewer, and tertiary branch is absent; its forewings are much shorter, so that the difference in wing lengths between these two genera is more than 10 mm. Besides, the specimen of the new *Angustitermes* species is from the upper Cretaceous while the three *Blattotermes* species are from the Cenozoic: *Blattotermes neoxenus* Riek, 1952 and *Blattotermes wheeleri* (Collins, 1925) are from Eocene, and *Blattotermes massiliensis* Nel, 1986 is from Oligocene (Collins 1925; Riek 1952; Nel 1986; Thorne et al. 2000; Krishna et al. 2013b).

***Angustitermes reflexus* Jiang, Z.Zhao & Ren, gen. et sp. nov.**
https://zoobank.org/A0343631-5430-4D81-9F18-F3E5AECB4071
Figs 1–3

Type material. *Holotype*. Myanmar • Imago♀; Kachin State, Hukawng Valley; one imago (abdomen fragmentary); Kachin amber; CNU-TER-BU-2017005 (Figs 1–3).

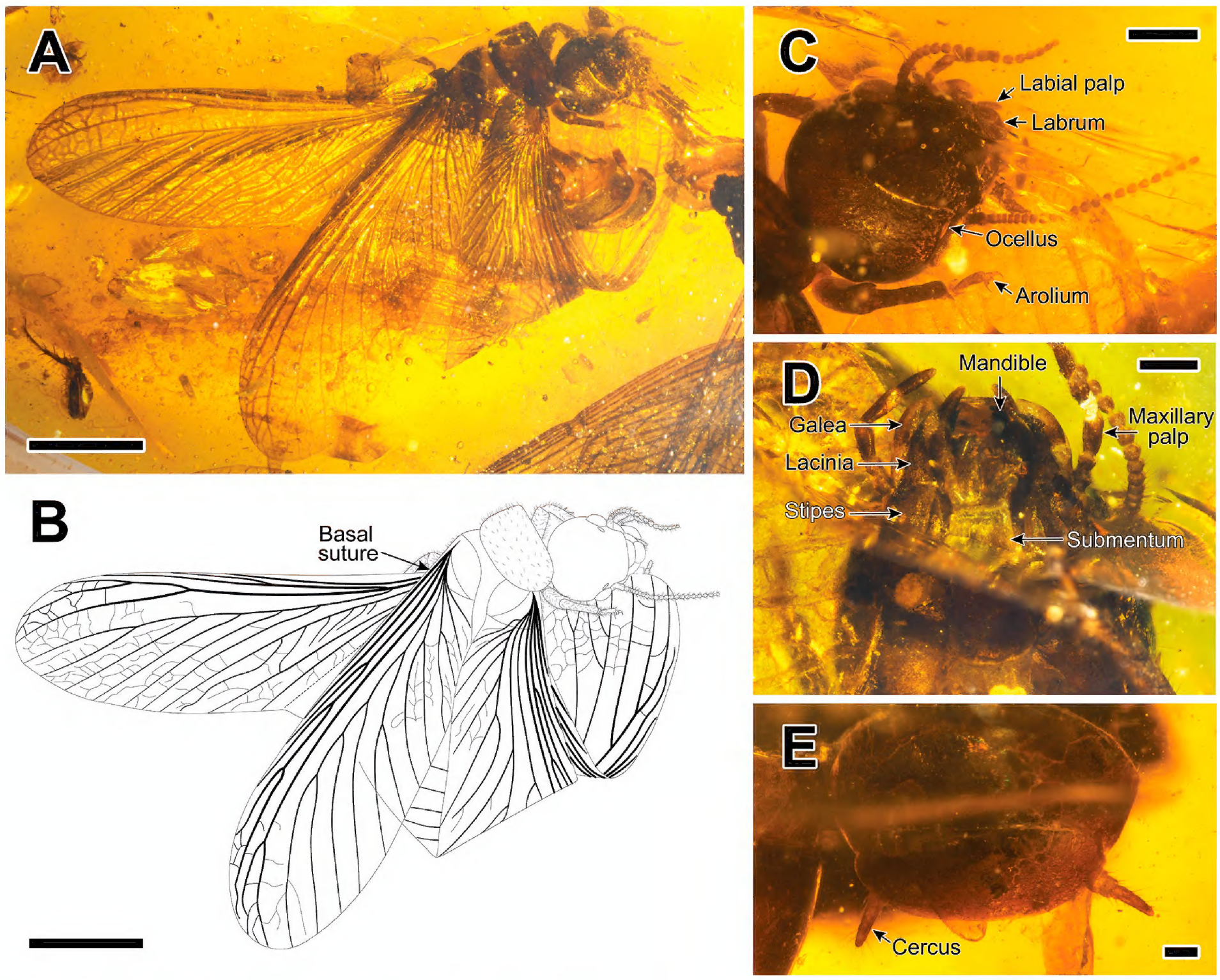

Figure 1. Photographs and drawing of *Angustitermes reflexus* gen. et sp. nov., holotype specimen CNU-TER-BU-2017005 (female imago) **A** habitus (dorsal view) **B** drawing of habitus (dorsal view) **C** head in dorsal view **D** head in ventral view **E** cerci in dorsal view. Scale bars: 4.0 mm (**A, B**); 1.0 mm (**C**); 0.5 mm (**D**); 0.2 mm (**E**).

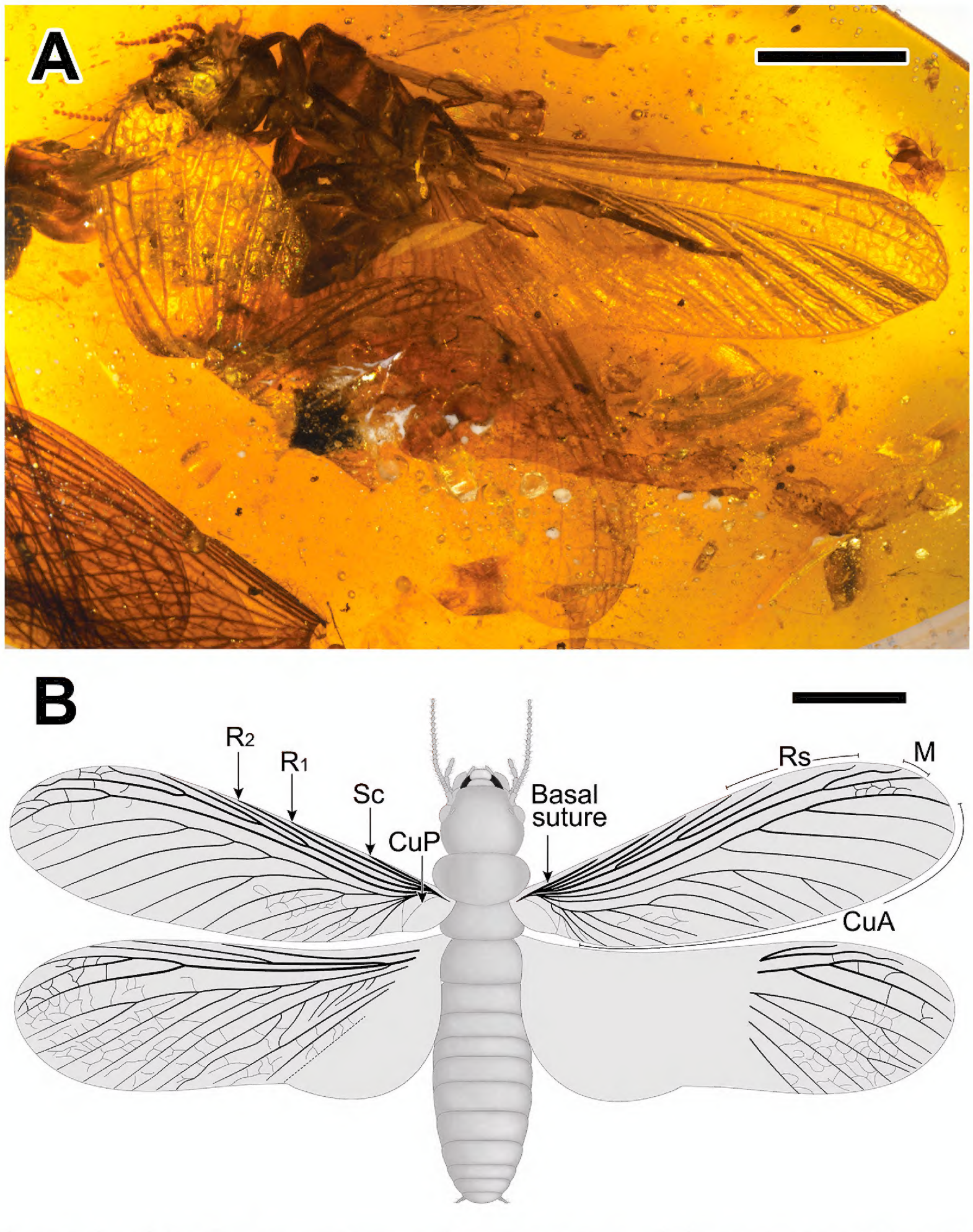

Figure 2. Photograph and drawing of *Angustitermes reflexus* gen. et sp. nov., holotype specimen CNU-TER-BU-2017005 (female imago) **A** habitus (ventral view) **B** partial reconstruction with wings unfolded. Scale bars: 4.0 mm (**A**); 4.0 mm (**B**).

Etymology. The specific name, *reflexus*, means "fold", which is in reference to the fact that the right forewing and right hindwing of the holotype are folded. The gender is masculine to match gender of the genus.

Locality. The specimen was collected from the upper Cretaceous (Cenomanian) deposits of the Hukawng Valley, Kachin State, northern Myanmar.

Diagnosis. As for the genus.

Description. Imago: head length 3.38 mm, width 2.99 mm (excluding sizes of compound eyes), with sparse setae; labrum sclerotized, connecting to anteclypeus, width longer than length, anterior margin with short setae; apical tooth of mandibles not reaching the apex of labrum, first marginal tooth and apical tooth of left mandible divided in acute angle, other marginal teeth not visible; width of

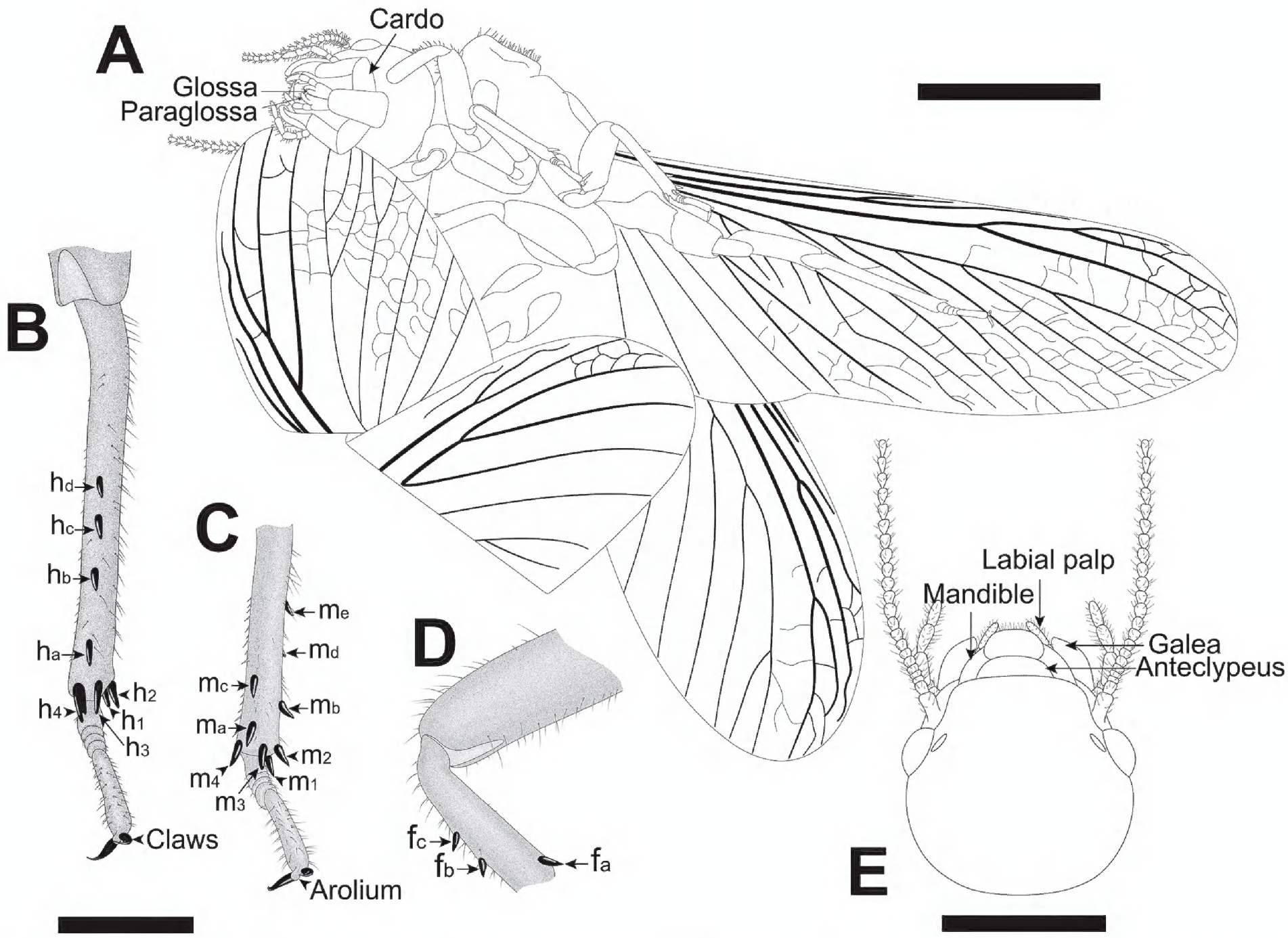

Figure 3. Drawings of *Angustitermes reflexus* gen. et sp. nov., holotype specimen CNU-TER-BU-2017005 (female imago) **A** drawing of habitus (ventral view) **B–D** drawings of femur, tibia, tarsi, arolium and claw of left hind leg, mid-leg and fore-leg, respectively **E** drawing of head in dorsal view. Scale bars: 4.0 mm (**A**); 0.5 mm (**B, C, D**); 2.0 mm in (**E**).

anteclypeus and postclypeus much longer than length; antenna with 22 articles; compound eyes hemispheric, slightly flat, diameter about 0.67 mm, lying on the middle position of the head, ommatidia diameter about 0.02 mm. Pronotum pilous, width about 3.35 mm, centraxonial length 1.97 mm, almost breaking away from the head. Wings long and broad with apex rounded, length 13.91 mm (excluding forewing scale), scale length 2.17 mm, wing width 5.02 mm; reticulated veins obviously pigmented among radial field and medial field, basal 5/8 of right hind wing hidden under right forewing. **Forewing:** scales with sparse setae, humeral margin convex, with weakly arched lobe present, basal suture curved; Sc simple, terminating on basal quarter of wing length; R with two branches in scale, terminating along anterior wing margin at half wing length; Radial field occupying about 1/8 wing area, left forewing with four branches, first branching at basal 1/3 of wing length, right forewing with three branches, first branching at basal 1/4 of wing length; M with two branches, branching at apical 1/5 of forewing; right CuA first branching in scale, occupying about 3/4 right forewing with three main branches, the branch near M vein branching at 1/2 of the wing length, the next branch branching near the middle of the wing to the base, and the branch near posterior margin branching in scale. **Hind wing:** basal suture not visible; large anal lobe present; left Rs with two branches branching from M at base; M with three branches. **Legs:** different degrees of damages to the legs, the left pro-

tarsus not preserved and the distal part of protibia not visible, the right mesotrochanter expanded and ruptured, and the large area of the left metacoxa broken; tibial spurs and spines not serrated. **Abdomen:** abdomen fragmentary, some of the detached abdominal segments can be observed, including the distal abdominal segments with a pair of cerci. Cerci trimerous; abdominal styli absent.

Genus *Mastotermes* Froggatt, 1897

***Mastotermes reticulatus* Jiang, Z. Zhao & Ren, sp. nov.**
https://zoobank.org/E9A4A732-D930-4B28-B22E-41507EA2C357
Fig. 4

Type material. *Holotype*. Myanmar • Kachin State, Hukawng Valley; forewing (margin partly missing) only; Kachin amber; CNU-TER-BU-2017006 (Fig. 4).

Etymology. Latin, *reticulatus*, meaning "reticulate", which is in reference to the well-developed and clearly recognizable reticulated veins of holotype.

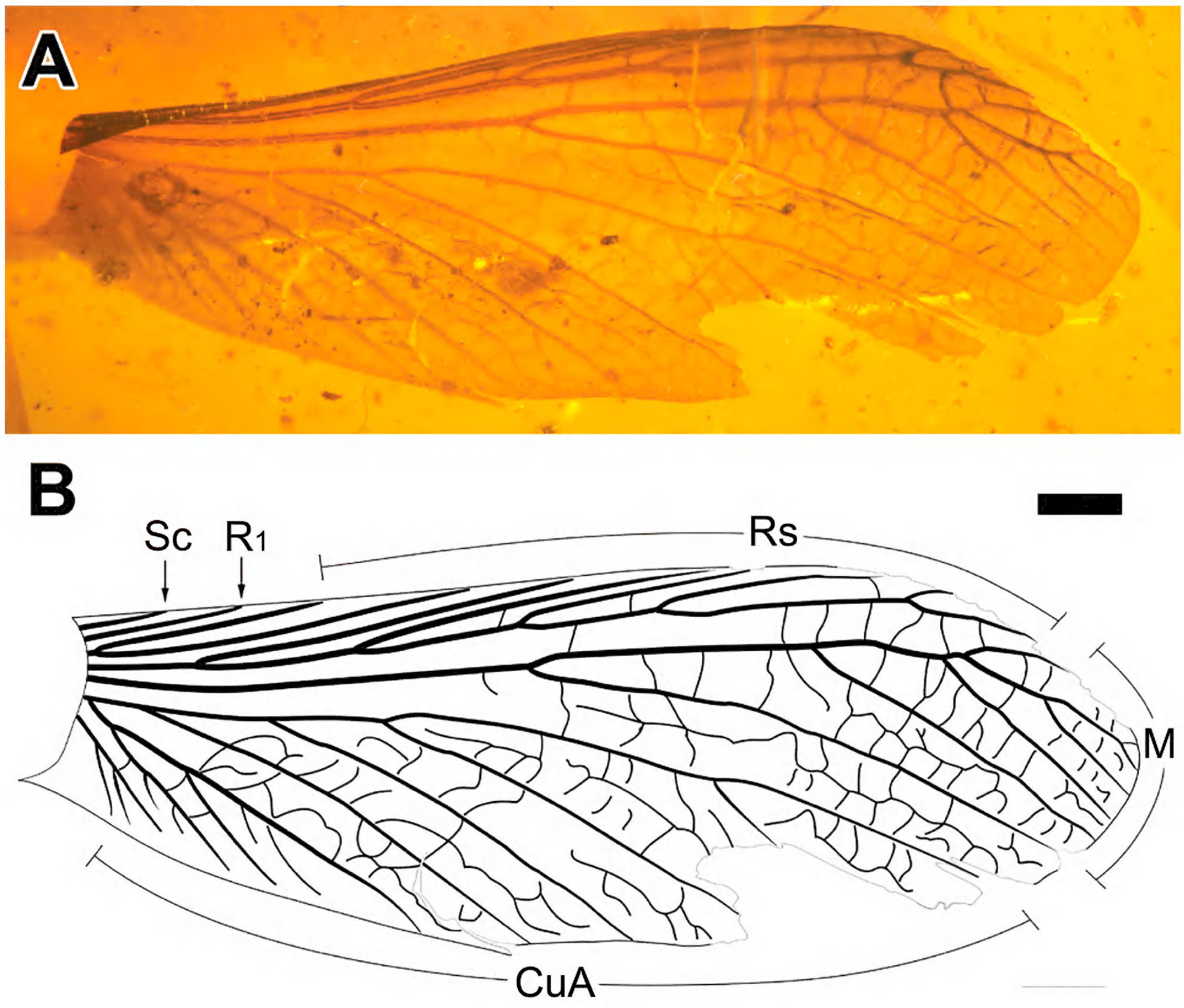

Figure 4. Photograph and drawing of *Mastotermes reticulatus* sp. nov., holotype specimen CNU-TER-BU-2017006 (isolated forewing) **A** photograph of forewing **B** drawing of forewing (with upturned part flattened). Scale bar: 1.0 mm (**A, B**).

Locality. The specimen was collected from the upper Cretaceous (Cenomanian) deposits of the Hukawng Valley, Kachin State, northern Myanmar.

Diagnosis. Forewing: wing length (excluding forewing scale) about three times as long as wide; forewing scale large; heavily reticulated, irregular bilayer structure in M and CuA, cross veins between Rs and M obvious; Sc, R, Rs, and M thickened, strongly sclerotized and obviously pigmented; Sc and R_1 simple and short; Rs with seven or eight branches, with secondary branches, running parallel to costal margin; M with six branches, first branch of M arising at forewing mid-length, secondary branches present, medial field encompassing wing apex, angle of branches and main vein gradually increasing.

Description. Forewing: forewing length (excluding forewing scale) 13.2 mm, width about 4.7 mm; suture length about 2.3 mm, strongly arched, making a sharp angle with posterior margin; distal costal margin slightly missing, posterior margin partially missing because of abrasion of the amber; base of costal margin rolled up, making the Sc and R poorly visible; Sc length 1.0 mm; R_1 length 2.0 mm, Rs with eight branches; M slightly closer to Rs than to CuA, encompassing wing apex, six branches visible, angle of branches and main vein gradually increasing, so that branches terminate closely on margin, first branch of M arising at forewing mid-length, second branch arising at about distal third of forewing length, and base of third branch close to fourth branch with secondary branch.

Remarks. The forewing of *Mastotermes reticulatus* sp. nov. is similar to that of *Mastotermes monostichus* Zhao, Eggleton & Ren, 2019, but there are some differences; the Sc, R, and Rs of *Mastotermes reticulatus* sp. nov. are closer, and there are fewer secondary branches, which makes the Rs veins parallel to the costal margin, instead of gradually narrowing as in *M. monostichus*. Compared with *M. monostichus*, the M vein of *M. reticulatus* sp. nov. is even more irregular and with fewer branches (Fig. 4). These different characteristics indicate that they are not the same species.

Discussion

The number of antennal articles in *Angustitermes reflexus* gen. et sp. nov. is only 22 (Fig. 2B), which is fewer than in most mastotermitids, especially the range of 29–32 of the extant *Mastotermes darwiniensis* (Krishna et al. 2013a), even though the antennae of many fossil termites are incompletely preserved. Another mastotermitid, *Mastotermes minutus* Nel & Bourguet, 2006 (Nel and Bourguet 2006), which was described from Early Eocene amber of Oise (France), has the fewest antennal articles, with only 20. Other mastotermitids that have been reported with complete antennae have more than 24 antennal articles. In addition to the antennae and the synapomorphies of mastotermitids, there are many similarities between *Mastotermes minutus* and *Angustitermes reflexus* gen. et sp. nov.: an ocellus is present, which indicates that they belong to the same subfamily; M of the hind wing branches from Rs, close to the wing scale; meso- and metatibiae have at least three lateral spines; tibial spurs are 3–4–4; and an arolium is present. However, these species also have some differences: the M vein of *Angustitermes reflexus* gen. et sp. nov. is closer to Rs than Cu (Fig. 2B), while the M vein of *Mastotermes minutus* is closer to Cu than to Rs. In terms of geological time, the number of antennal articles within Mastotermitidae seems to

change from many (plesiomorphic state) to few and then back to many. Further phylogenetic analysis with more fossil mastotermitids may clarify the specific trend of the evolution of the number of antennal articles in Mastotermitidae.

The sclerotized vein M of the forewings in *Angustitermes reflexus* gen. et sp. nov. are relatively simple, with only two branches and the medial fields, located in the anterior third, compressed. Concurrently, the distal-most branches of CuA, which end at the wing apex, are also thick and sclerotized, similar to M, and stronger than the other branches of CuA (Figs 2, 3A). This is opposite in the wings of *Mastotermes reticulatus* sp. nov., *Anisotermes xiai*, and *Mastotermes monostichus*, which have multibranched M in the forewing, with the basal-most branches gradually tapering and unsclerotized. Mastotermitids share a synapomorphy: the Sc, R, Rs, and M veins are thicker and much sclerotized than CuA (Engel et al. 2009; Zhao et al. 2019). The synapomorphy tends to indicate the overall degree of sclerotization present in each vein, and some branches with different locations may show different degrees of thickness and sclerotization.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Yurong Jiang: data curation, formal analysis, methodology, writing-original draft; Xinru Deng: data curation, formal analysis, methodology; Chungkun Shih: formal analysis, writing-review and editing; Yunyun Zhao: formal analysis, writing-review and editing; Dong Ren: data curation, writing-review, supervision; Zhipeng Zhao: writing-review and editing, project administration, supervision.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Beccaloni G, Eggleton P (2013) Order Blattodea. In: Zhang Z-Q (Ed.) Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013). Zootaxa 3703(1): 46–48. https://doi.org/10.11646/zootaxa.3703.1.10

Bezerra FI, Mendes M, De Souza O (2020) New record of Mastotermitidae from Fonseca Basin, Eocene-Oligocene boundary of southeastern Brazil. Biologia 75(11): 1881–1890. https://doi.org/10.2478/s11756-020-00441-x

Bignell DE, Roisin Y, Lo N [Eds] (2011) Biology of Termites: a Modern Synthesis. Springer Science+Business Media, Springer Dordrecht, [xiv +] 576 pp. https://doi.org/10.1007/978-90-481-3977-4

Breznak JA, Brune A (1994) Role of microorganisms in the digestion of lignocellulose by termites. Annual Review of Entomology 39(1): 453–487. https://doi.org/10.1146/annurev.en.39.010194.002321

Bucek A, Šobotník J, He S, Shi M, McMahon DP, Holmes EC, Roisin Y, Lo N, Bourguignon T (2019) Evolution of termite symbiosis informed by transcriptome-based phylogenies. Current Biology 29(21): 3728–3734. https://doi.org/10.1016/j.cub.2019.08.076

Collins RL (1925) A lower Eocene termite from Tennessee. American Journal of Science 5(53): 406–410. https://doi.org/10.2475/ajs.s5-9.53.406

Eggleton P, Beccaloni G, Inward D (2007) Response to Lo et al. Biology Letters 3(5): 564–565. https://doi.org/10.1098/rsbl.2007.0367

Engel MS (2008) Two new termites in Baltic amber (Isoptera). Journal of the Kansas Entomological Society 81(3): 194–203. https://doi.org/10.2317/JKES-0802.01.1

Engel MS, Grimaldi DA, Krishna K (2007) A synopsis of Baltic amber termites (Isoptera). Stuttgarter Beitrage zur Naturkunde. Serie B, Geologie und Palaontologie 372: 1–20.

Engel MS, Grimaldi DA, Krishna K (2009) Termites (Isoptera): Their phylogeny, classification, and rise to ecological dominance. American Museum Novitates 3650(3650): 1–27. https://doi.org/10.1206/651.1

Engel MS, Currano ED, Jacobs BF (2015) The first mastotermitid termite from Africa (Isoptera: Mastotermitidae): a new species of *Mastotermes* from the early Miocene of Ethiopia. Journal of Paleontology 89(6): 1038–1042. https://doi.org/10.1017/jpa.2015.73

Froggatt WW (1897) Australian Termitidae. Part II. Proceedings of the Linnean Society of New South Wales 21(4)[1896]: 510–552[+ 2 pls]. https://doi.org/10.5962/bhl.part.8483

Inward D, Beccaloni G, Eggleton P (2007) Death of an order: A comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biology Letters 3(3): 331–335. https://doi.org/10.1098/rsbl.2007.0102

Jiang RX, Zhang HR, Eldredge KT, Song XB, Li YD, Tihelka E, Huang DY, Wang S, Engel MS, Cai CY (2021) Further evidence of Cretaceous termitophily: description of new termite hosts of the trichopseniine *Cretotrichopsenius* (Coleoptera: Staphylinidae), with emendations to the classification of lower termites (Isoptera). Palaeoentomology 4(4): 374–389. https://doi.org/10.11646/palaeoentomology.4.4.13

Jouault C, Legendre F, Grandcolas P, Nel A (2021) Revising dating estimates and the antiquity of eusociality in termites using the fossilized birth–death process. Systematic Entomology 46(3): 592–610. https://doi.org/10.1111/syen.12477

Jouault C, Engel MS, Legendre F, Huang D, Grandcolas P, Nel A (2022) Incrementing and clarifying the diversity and early evolution of termites (Blattodea: Isoptera). Zoological Journal of the Linnean Society 196(2): 608–629. https://doi.org/10.1093/zoolinnean/zlac064

Krishna K, Emerson AE (1983) A new fossil species of termite from Mexican amber, *Mastotermes electromexicus* (Isoptera, Mastotermitidae). American Museum Novitates 2767: 1–8.

Krishna K, Grimaldi DA (1991) A new fossil species from Dominican amber of the living Australian termite genus *Mastotermes* (Isoptera, Mastotermitidae). American Museum Novitates 3021: 1–10.

Krishna K, Grimaldi DA, Krishna V, Engel MS (2013a) Treatise on the Isoptera of the world: Basal families. Bulletin of the American Museum of Natural History 377(7): 1–196. https://doi.org/10.1206/377.1

Krishna K, Grimaldi DA, Krishna V, Engel MS (2013b) Treatise on the Isoptera of the world: Basal families. Bulletin of the American Museum of Natural History 377(7): 223–246. https://doi.org/10.1206/377.2

Legendre F, Nel A, Svenson GJ, Robillard T, Pellens R, Grandcolas P (2015) Phylogeny of Dictyoptera: Dating the origin of cockroaches, praying mantises and termites with molecular data and controlled fossil evidence. PLOS ONE 10(7): e0130127. https://doi.org/10.1371/journal.pone.0130127

Lo N, Engel MS, Cameron S, Nalepa CA, Tokuda G, Grimaldi D, Kitade O, Krishna K, Klass KD, Maekawa K, Miura T, Thompson GJ (2007) Save Isoptera: A comment on Inward et al. Biology Letters 3(5): 562–563. https://doi.org/10.1098/rsbl.2007.0264

Nalepa CA, Lenz M (2000) The ootheca of *Mastotermes darwiniensis* Froggatt (Isoptera: Mastotermitidae): homology with cockroach oothecae. Proceedings of the Royal Society B, Biological Sciences 267(1454): 1809–1813. https://doi.org/10.1098/rspb.2000.1214

Nel A (1986) Sur trois espèces nouvelles de termites fossiles du Stampien d'Aix-en-Provence (Bouches-du-Rhône) (Dictyoptera, Hodotermitidae, Mastotermitidae). Entomologiste (Paris) 42(5): 271–278.

Nel A, Bourguet E (2006) Termite of the Early Eocene amber of France (Isoptera: Mastotermitidae, Kalotermitidae). Neues Jahrbuch für Geologie und Palдontologie. Monatshefte 2006(2): 101–115. https://doi.org/10.1127/njgpm/2006/2006/101

Riek EF (1952) Fossil insects from the Tertiary sediments at Dinmore, Queensland. Papers from the Department of Geology, University of Queensland 4(2): 17–22.

Sanderson MG (1996) Biomass of termites and their emissions of methane and carbon dioxide: A global database. Global Biogeochemical Cycles 10(4): 543–557. https://doi.org/10.1029/96GB01893

Schlüter T (1989) Neue Daten über harzkonservierte Arthropoden aus dem Cenomanium NW-Frankreichs. Documenta Naturae (München) 56(5): 59–70[+ 6 pls].

Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei WY, Li QL, Li XH (2012) Age constraint on Myanmar amber based on U-Pb dating of zircons. Cretaceous Research 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Sugimoto A, Bignell DE, MacDonald JA (2000) Global impact of termites on the carbon cycle and atmospheric trace gases. In: Abe T, Bignell DE, Higashi M (Eds) Termites: evolution, sociality, symbioses, ecology, 409–435. Kluwer Academic Publishers, Dordrecht, [xxii +] 466 pp. https://doi.org/10.1007/978-94-017-3223-9_19

Thompson GJ, Kitade O, Lo N, Crozier RH (2000) Phylogenetic evidence for a single ancestral origin of a "true" worker caste in termites. Journal of Evolutionary Biology 13(6): 869–881. https://doi.org/10.1046/j.1420-9101.2000.00237.x

Thorne BL, Grimaldi DA, Krishna K (2000) Early Fossil History of the Termites. In: Abe T, Bignell DE, Higashi M (Eds) Termites: Evolution, Sociality, Symbioses, Ecology. Springer, Dordrecht, 77–93. https://doi.org/10.1007/978-94-017-3223-9_4

Tuma J, Eggleton P, Fayle TM (2020) Ant-termite interactions: An important but under-explored ecological linkage. Biological Reviews of the Cambridge Philosophical Society 95(3): 555–572. https://doi.org/10.1111/brv.12577

Vršanský P, Aristov D (2014) Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence for the longevity of their earliest genera. European Journal of Entomology 111(1): 137–141. https://doi.org/10.14411/eje.2014.014

Wappler T, Engel MS (2006) A new record of *Mastotermes* from the Eocene of Germany (Isoptera: Mastotermitidae). Journal of Paleontology 80(2): 380–385. https://doi.org/10.1666/0022-3360(2006)080[0380:ANROMF]2.0.CO;2

Xiao B, Chen AH, Zhang YY, Jiang GF, Hu CC, Zhu CD (2012) Complete mitochondrial genomes of two cockroaches, *Blattella germanica* and P*eriplaneta americana*, and the phylogenetic position of termites. Current Genetics 58(2): 65–77. https://doi.org/10.1007/s00294-012-0365-7

Zhao ZP, Eggleton P, Yin XC, Gao TP, Shih CK, Ren D (2019) The oldest known mastotermitids (Blattodea: Termitoidae) and phylogeny of basal termites. Systematic Entomology 44(3): 612–623. https://doi.org/10.1111/syen.12344

Zhao ZP, Yin XC, Shih CK, Gao TP, Ren D (2020) Termite colonies from mid-Cretaceous Myanmar demonstrate their early eusocial lifestyle in damp wood. National Science Review 7(2): 381–390. https://doi.org/10.1093/nsr/nwz141

Zhao ZP, Shih CK, Gao TP, Ren D (2021) Termite communities and their early evolution and ecology trapped in Cretaceous amber. Cretaceous Research 117: 104612. https://doi.org/10.1016/j.cretres.2020.104612